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Carbon accumulation along a stand development sequence of *Nothofagus antarctica* forests across a gradient in site quality in Southern Patagonia

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ABSTRACT

Above- and below-ground C pools were measured in pure even-aged stands of *Nothofagus antarctica* (Forster f.) Oersted at different ages (5–220 years), crown and site classes in the Patagonian region. Mean tissue C concentration varied from 46.3% in medium sized roots of dominant trees to 56.1% in rotten wood for trees grown in low quality sites. Total C concentration was in the order of: heartwood > rotten wood > sapwood > bark > small branches > coarse roots > leaves > medium roots > fine roots. Sigmoid functions were fitted for total C accumulation and C root/shoot ratio of individual trees against age. Total C accumulated by mature dominant trees was six times greater than suppressed trees in the same stands, and total C accumulated by mature dominant trees grown on the best site quality was doubled that of those on the lowest site quality. Crown classes and site quality also affected the moment of maximum C accumulation, e.g. dominant trees growing on the worse site quality sequestered 0.73 kg C $tree^{-1}$ $year^{-1}$ at 139 years compared to the best site where 1.44 kg C $tree^{-1}$ $year^{-1}$ at 116 years was sequestered. C root/shoot ratio decreased over time from a maximum value of 1.3–2.2 at 5 years to a steady-state asymptote of 0.3–0.7 beyond 60 years of age depending on site quality. Thus, root C accumulation was greater during the regeneration phase and for trees growing on the poorest sites. The equations developed for individual trees have been used to estimate stand C accumulation from forest inventory data. Total stand C content ranged from 128.0 to 350.9 Mg C ha^{-1}, where the soil C pool represented 52–73% of total ecosystem C depending on age and site quality. Proposed equations can be used for practical purposes such as estimating the impact of silvicultural practices (e.g. thinning or silvopastoral systems) on forest C storage or evaluating the development of both above- and below-ground C over the forest life cycle for different site qualities for accurate quantification of C pools at regional scale.

1. Introduction

Data on carbon (C) storage in forests and different tree components are essential for understanding the importance of rapidly increasing level of CO_2 in the atmosphere and its potential effect on global climate change. In South America, mean annual temperature is predicted to increase by 3–4 °C in both summer and winter between 30° and 55° SL (Manabe and Wetherald, 1987). Such an increase would have significant effects on *Nothofagus* forests. In this context, secondary indigenous forests are considered efficient C sink ecosystems. *Nothofagus antarctica* (Forster f.) Oersted (ñire), one of the main deciduous native species in the Patagonian region (Argentina), covers 7500 km^2 over a wide latitudinal (from 36°25′ to 54°53′SL) and altitudinal (near sea level to 2000 m.a.s.l.) distribution. These forests occur naturally in different habitats such as poorly drained sites at low elevations, exposed windy areas with shallow soils, depressions under cold air influence, or in drier eastern sites near the Patagonian steppe (Veblen et al., 1996). These forests provide a range of wood products including poles, firewood and timber for rural construction purposes.

Several studies have shown the importance of factors such as forest type, climate, soil properties, site quality, or stand productivity on C storage of forest ecosystems (Dixon et al., 1994; Bert and Danjon, 2006). Site quality for *N. antarctica* ranges from tall trees up to 15 m in dominant height on the best sites to shrubby trees of 2 m tall on rocky, xeric and exposed sites, and also in poorly drained sites (peat bog) (Veblen et al., 1996). Previous research has highlighted the importance of stand age on the magnitude of C pools in both forest biomass and forest floor pools (Grigal and Ohmann, 1992; Silvester and Orchard, 1999; Davis et al., 2003). Large-scale canopy disturbance in *N. antarctica* forests may occur as a result of tectonic activity, blowdown, snow avalanches or fire. This results in

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Table 1
Mean dasometric (±standard deviation) characteristics of sampled *Nothofagus antarctica* stands grown at three sites qualities in Southern Patagonia.

Growth phase	Age class (years)	Density (trees ha^{-1})	Height (m)	DBH (m)	Basal area (m^2 ha^{-1})	% Crown classes			
						D	C	I	S
Site Class III									
Regeneration	5–20	35,050 ± 2459	1.5 ± 0.5	0.028 ± 0.004	38.3 ± 2.3	24	26	30	20
Optimal growth	21–110	5820 ± 1088	5.8 ± 0.8	0.095 ± 0.03	44.6 ± 3.1	28	30	28	14
Mature	111–235	420 ± 89	10.2 ± 1.5	0.285 ± 0.07	32.2 ± 2.4	40	28	25	7
Site Class IV									
Regeneration	5–20	23,500 ± 1504	1.2 ± 0.4	0.030 ± 0.002	40.5 ± 2.6	21	17	28	34
Optimal growth	21–110	4950 ± 980	4.3 ± 0.7	0.115 ± 0.01	51.2 ± 3.4	30	26	23	21
Mature	111–220	460 ± 55	7.5 ± 1.6	0.256 ± 0.06	30.8 ± 1.8	35	30	22	13
Site Class V									
Regeneration	5–20	26,120 ± 8100	1.1 ± 0.6	0.020 ± 0.003	32.3 ± 3.1	20	24	25	31
Optimal growth	21–110	3330 ± 1200	3.4 ± 0.8	0.108 ± 0.02	29.3 ± 2.9	25	28	24	23
Mature	111–200	440 ± 35	5.3 ± 0.7	0.202 ± 0.05	25.4 ± 2.7	36	27	23	14

Crown classes = D: dominant trees, C: codominant trees, I: intermediate trees, S: suppressed trees.
Site Class III: stands where the mean total height of dominant mature tree (H) reach 10.2 m, Site Class IV: H = 7.8 m, Site Class V: H = 5.3 m.

abundant regeneration (~100,000 seedlings ha^{-1} less than 1 m tall, up to 20 years of age) followed by self-thinning due mainly to light competition (Veblen et al., 1996) resulting in a final stand density of ~200–350 trees ha^{-1} at mature stages (more than 180 years of age).

It is important to emphasize that many researchers have only focused on above-ground carbon sequestration (Davis et al., 2003). However, roots in forest ecosystems can contribute up to two times more biomass than above-ground components in young growth phases (Peri et al., 2006).

There are few studies of above- and below-ground pools of C storage in Patagonian *Nothofagus* forests that provide an understanding about ecosystem functionality (Peri et al., 2006, 2008) and the consequences of different disturbance and management regimes, and there are no reports of above- and below-ground carbon accumulation related to stand age and degree of canopy suppression. In this context, forest ecosystem pools and fluxes of C are strongly affected by forest management (Finér et al., 2003). We hypothesize that C storage in tree components (leaves, stems, branches, and roots) and forest floor will change as a result of different forest structures determined by the proportion of crown classes, development stages (age) and the site quality where trees grow. Therefore, the aim of this study was to quantify the amount and dynamics of C in both above- and below-ground components for an age sequence and among crown classes for individual trees grown at different site qualities of deciduous *N. antarctica* forests in Southern Patagonia.

2. Materials and methods

2.1. Study sites and stand characteristics

This study was conducted in natural stands of *N. antarctica* forest growing in the southern west of Santa Cruz province (Argentina) at three site qualities (Lencinas et al., 2002): Site Class III (SC III) where the mean total height of dominant mature tree (H) reached 10.2 m (51°13′21″SL, 72°15′34″WL), Site Class IV (SC IV) where H reached 7.8 m (51°34′10″SL, 72°14′21″WL), and Site Class V (SC V) which represented a marginal site where H reached 5.3 m (51°40′59″SL, 72°15′56″WL). These stands are part of a larger experiment described by Peri et al. (2006, 2008) where the biomass and nutrients in both above- and below-ground components of *N. antarctica* forests have been studied. Regional climate is cold temperate and sub-humid with a mean annual temperature of 6.5 °C and a long-term annual rainfall of 300 mm. Soils were classified as Mollisols.

In each of the three study areas of 400 km^2, three pure stands corresponding to different development phases (regeneration phase 5–20 years of age, optimal growth phase 21–110 years of age and mature phase 111–220 years of age) were selected. In each stand, three circular plots of 500 m^2 were randomly located in each stand to characterize the forest structure (Table 1). Mean stand density ranged from 35,050 trees ha^{-1} in the regeneration phase to 420 trees ha^{-1} in the mature phase. In the study stands, mean dominant height (H) ranged from 1.1 to 10.2 m, mean diameter at 1.3 m height (DBH) from 0.02 to 0.28 m and mean basal area from 25.4 to 51.2 m^2 ha^{-1}. The proportion of dominant trees increased and suppressed trees decreased with age (Table 1).

2.2. Soil C sampling

Thirty bulked soil sample cores from each stand at four different depths corresponding to observe root distribution (forest floor litter from 0 to 1 cm, organic horizon from 1 to 6 cm, mineral horizon I from 5 to 30 cm, mineral horizon II from 30 to 60 cm) were taken at random (Table 2). Soil samples were kept at 2 °C until further processed. The litter layer and organic samples were oven-dried at 70 °C and ground with a Wiley mill to pass a 1 mm mesh. The mineral soil samples were air dried and passed through a 2 mm sieve. Soil bulk density was measured from the weight of the soil per unit volume (g cm^{-3}) given on an oven-dry basis. C concentration was determined by dry combustion using a LECO analyser. The content of soil C for each sampling depth was calculated by applying the C concentration to the soil bulk density of a particular depth.

2.3. Tree C determination

For each stand, ninety-six trees of different age classes corresponding to different stand development phases (regeneration: 5–20 years, optimal growth: 21–110 years and mature: 111–220 years) were randomly selected. Within each age class, eight trees of each crown class (dominant, codominant, intermediate and suppressed) were sampled. Thus, a total of 288 trees were sampled (3 site quality class × 3 development stand stages × 4 crown classes × 8 replicates). For each tree, total height and DBH were measured, and the stem was cut at 0.1 m (stump), 1.3 m and every 1 m up to an end diameter of 10 mm after the harvesting to calculate volume of heartwood, sapwood, bark and rotten wood components using the Smalian formula. Each tree was separated into the following components: leaves; small branches (diameter < 10 mm) and coarse branches (>10 mm) with bark; stem components including sapwood, heartwood and bark; and roots with bark classified as fine (diameter < 2 mm), medium (<30 mm) or coarse (>30 mm).

Table 2
Mean soil properties in sampled *Nothofagus antarctica* forests grown at different site classes in Southern Patagonia, Argentina (standard deviation in parenthesis, $n = 3$).

Soil horizons	Site Class III				Site Class IV				Site Class V			
	Litter	Organic horizon	Mineral horizon I	Mineral horizon II	Litter	Organic horizon	Mineral horizon I	Mineral horizon II	Litter	Organic horizon	Mineral horizon I	Mineral horizon II
Depth (cm)	0–2	2–6	6–20	20–60	0–1	1–5	5–30	30–60	0–1	1–4	4–20	20–50
Clay (%)	–	–	10	15	–	–	20	20	–	–	26	25
Silt (%)	–	–	37	24	–	–	30	60	–	–	23	20
Sand (%)	–	–	53	61	–	–	50	20	–	–	51	55
Bulk density ($g\,cm^{-3}$)	0.07 (0.02)	0.47 (0.06)	0.79 (0.12)	1.04 (0.16)	0.10 (0.01)	0.39 (0.05)	1.14 (0.19)	1.29 (0.14)	0.09 (0.01)	0.63 (0.07)	0.97 (0.16)	1.05 (0.09)
Carbon concentration (%)	47.2 (6.11)	16.0 (2.04)	6.0 (0.71)	2.3 (0.22)	50.8 (0.78)	14.2 (0.24)	2.1 (0.15)	0.4 (0.07)	49.1 (5.53)	9.4 (1.12)	3.2 (0.64)	0.5 (0.06)
Carbon content ($Mg\,ha^{-1}$)	6.6 (0.8)	30.1 (2.8)	66.4 (7.8)	95.7 (8.4)	5.8 (0.8)	22.1 (0.3)	59.8 (6.1)	15.5 (1.1)	4.4 (0.5)	17.8 (2.1)	49.7 (6.3)	15.8 (2.2)

Site Class III: stands where the mean total height of dominant mature tree (H) reach 10.2 m, Site Class IV: H = 7.8 m, Site Class V: H = 5.3 m.

Three samples of each component in every tree were taken for dry weight and C analysis. For coarse branches and stem, three cross-sectional discs of 30 mm at different lengths were taken and separated into their component pool (heartwood, sapwood, bark and rotten wood) to determine density for biomass calculations. All small branches, leaves and dead branches from each sampled tree were separated and weighed fresh. Roots from individual trees were excavated to a depth of 0.5 m for SC V and 0.6 m for SC III and SC IV (maximum rooting depth for all crown classes) in circular plots (radius ranged from 1.5 m for regeneration to 10.2 m for mature trees growing in SC III) centred on the stump of the sampled trees. These roots were sorted into diameter classes (fine < 2 mm, medium < 30 mm, coarse > 30 mm) and weighed in fresh. Subsamples were taken for oven drying to estimate biomass and C analysis. Although the fine root biomass was underestimated because it is difficult to assess the entire root system using the excavation method, we agree with Le Goff and Ottorini (2001) who reported that coarse roots contribute most to the total root biomass and that the fine fraction represents a very small part of the total root system. Therefore, the missing fine root biomass would not strongly influence the total estimated root biomass.

Samples from the three age classes in each site class were dried in a forced draft oven at 65 °C to constant weight and ground in a mill containing 1 mm stainless steel screen for C analysis. C concentrations were determined by dry combustion using a LECO analyser.

C accumulation of trees was estimated by multiplying C concentrations from chemical analysis and the mass of each biomass component (dry weight measurements). Age of each sample tree was obtained by counting rings at the stump (0.3 m from soil level). C accumulation was divided by tree age to establish the average annual rate at which C was accumulated by trees.

2.4. Statistical analysis

Total C accumulation and C root/shoot ratio functions were fitted using non-linear regression analysis. Different sigmoid functions (Chapman-Richard, Logistic, Weibull, Gompertz, Hill and Schumacher) were compared to fit total C accumulation against age and crown suppression classes. For C root/shoot ratio data, inverse functions were fitted against age. The selected functions were first estimated for each crown class based on individual trees in each stand. The parameters of these functions for each crown suppression classes were subjected to an analysis of variance (ANOVA) as a segregation indicator.

Comparisons of main factors (site, age and crown classes) were carried out by analyses of variance with the *F* test for C concentration and allocation. Significantly different averages were separated with standard error of means to evaluate least significant differences (LSD). All tests were evaluated at $P < 0.05$. Statistical analyses were carried out using the Genstat statistical package (Genstat 5—v.1997).

3. Results

3.1. Soil C

There were no significant differences in soil C pools for different age classes (data not shown) (Table 2). However, total C content in the soil profile varied according to the site quality, being 87.7, 103.2 and 198.8 $Mg\,C\,ha^{-1}$ for SC V, SC IV and SC III, respectively (Table 2). Soil C concentration increased from SC V to SC III thus influencing C content in organic and inorganic horizons (Table 2). The organic-layer C content ranged from 17.8 to 30.1 $Mg\,C\,ha^{-1}$ for SC V and SC III, respectively. C content in inorganic layers of SC III

Table 3
Mean carbon concentration in components of *Nothofagus antarctica* trees (data expressed as a percentage of dry matter) for different crown, age and site classes.

	Leaves	Small branches	Sapwood	Heartwood	Bark	Rotten wood	Roots		
							<2 mm	<30 mm	>30 mm
Age class									
5-20 years	48.9	50.1	50.3	51.6	49.9	51.5	46.8	47.0	49.1
21-110 years	49.8	50.5	51.7	53.2	51.8	52.5	48.2	47.7	50.2
111-235 years	50.2	51.6	52.4	54.2	52.0	53.2	48.8	48.7	51.0
Crown class									
Dominant	48.3	49.6	50.4	51.3	49.8	51.1	46.4	46.3	48.8
Codominant	49.3	50.1	51.2	52.5	50.5	51.7	47.3	47.2	49.4
Intermediate	50.0	51.1	51.5	53.5	51.7	52.6	48.5	48.3	50.5
Suppressed	50.8	52.0	53.0	54.7	52.9	54.1	49.4	49.3	51.5
Site class									
Site Class III	48.5	49.1	49.8	51.1	49.4	50.5	46.5	47.1	47.9
Site Class IV	49.1	49.6	50.2	52.8	50.7	51.6	47.3	47.7	48.2
Site Class V	51.3	53.4	54.4	55.1	53.6	56.1	49.9	48.5	54.2
Age class effect	ns (1.35)	ns (1.54)	(0.64)*	(0.88)*	(1.01)*	ns (1.82)	(0.45)*	ns (1.47)	(0.75)*
Crown class effect	(0.68)*	(0.58)*	(0.44)**	(0.73)***	(0.97)*	(1.07)**	(0.38)**	(0.81)**	(0.67)*
Site class effect	(0.54)*	(0.42)**	(0.37)***	(0.64)**	(0.55)**	(0.41)***	(0.57)*	ns (1.45)	(0.49)**
Interaction	ns (1.75)	ns (1.67)	(0.71)*	(0.92)*	(1.07)*	ns (1.91)	(0.52)*	ns (1.55)	(0.77)*

Site Class III: stands where the mean total height of dominant mature tree (H) reach 10.2 m, Site Class IV: H = 7.8 m, Site Class V: H = 5.3 m.
ns = non significative (standard error of differences of means in parentheses).
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

was more than twofold greater than the other site quality class. Similarly, litter C content was greater for the best site quality.

3.2. C concentration in the tree components

C concentration in each biomass pool component, except for medium roots, showed significant differences according to crown and site classes (Table 3). C concentration in components increased from dominant to suppressed trees and from trees grown in SC III to SC V. For example, mean C concentration in leaves was 48.3% in dominant trees and 50.8% in suppressed trees, and 48.5% in SC III and 51.3% in SC V.

C concentrations in leaves, small branches, rotten wood and medium root did not differ ($P > 0.05$) between trees of different ages (Table 3). C concentration of other biomass components (sapwood, heartwood, bark, fine and coarse roots) increased with increasing stand development.

C concentrations significantly varied between biomass pool components. Total C concentration generally graded in the following order: heartwood > rotten wood > sapwood > bark > small branches > coarse roots > leaves > medium roots > fine roots (Table 3).

3.3. Total C accumulation

A logistic function (Eq. (1)) with three parameters was used to estimate total C accumulation of individual trees.

$$Y = \frac{a}{1 + (x/b)^c} \qquad (1)$$

where Y = C of individual trees (kg); x = age (years); a, b and c are the estimated parameters and are provided in Appendix A.

Relationships between the total C content of *N. antarctica* and age for different crown and site classes are presented in Fig. 1. The ANOVA of parameters showed significant differences ($P < 0.05$) for each crown class. Total C accumulation over time followed the order: dominant > codominant > intermediate > suppressed trees. For example, dominant trees growing on SC IV had accumulated 164.6 kg C tree^{-1} after 160 years and suppressed trees only 23.1 kg C tree^{-1}. At 40 years of age these differences were 8.6, 6.1, 3.3 and 0.9 kg C tree^{-1} for dominant, codominant, intermediate and suppressed trees, respectively (Fig. 1b). Also, there was an effect of site quality of the stands on total C accumulation over time. For example, while the mean total C accumulated for dominant trees grown in SC V at 150 years was 108.9 kg C tree^{-1} (Fig. 1c), dominant trees growing on SC III had 206.8 kg C tree^{-1} (Fig. 1a).

The rate of C accumulation showed a parabolic relationship with tree age and increased to reach a maximum and then declined as tree age increased further (Fig. 2). Position in the canopy also affected the maximum value and shape of this response. For example, maximum accumulation rate for dominant trees growing on SC IV was 1.08 kg C tree^{-1} year^{-1} at 126 years and then declined to 0.84 kg C tree^{-1} year^{-1} at 220 years. In contrast, maximum accumulation rate for suppressed trees was 0.14 kg C tree^{-1} year^{-1} at 133 years (Fig. 2b). Also, the site quality modified the maximum values and the shape of the rate of C accumulation. While the maximum C accumulation rate of dominant trees growing on SC V was 0.73 kg C tree^{-1} year^{-1} at 139 years (Fig. 2c), for SC III it was 1.44 kg C tree^{-1} year^{-1} at 116 years (Fig. 2a).

3.4. Above- and below-ground C ratio

An inverse function (Eq. (2)) with two parameters described the C root/shoot ratio data better than others functions (data not shown).

$$y = a + \left(\frac{b}{x}\right) \qquad (2)$$

where y = C root/shoot ratio of individual trees (dimensionless); x = age (years); a and b are the estimated parameters.

There were no significant difference in the slope of the relationship between the C root/shoot ratio and age for different crown classes. Therefore, a single function was used for each site quality class. The parameters for each site class are given in Appendix B.

C root/shoot ratio decreased from maximum values of 2.2, 1.9 and 1.3 at 5 years to a steady-state asymptote of 0.7, 0.5 and 0.3 beyond 60 years of age, for trees grown in SC V, SC IV and SC III,

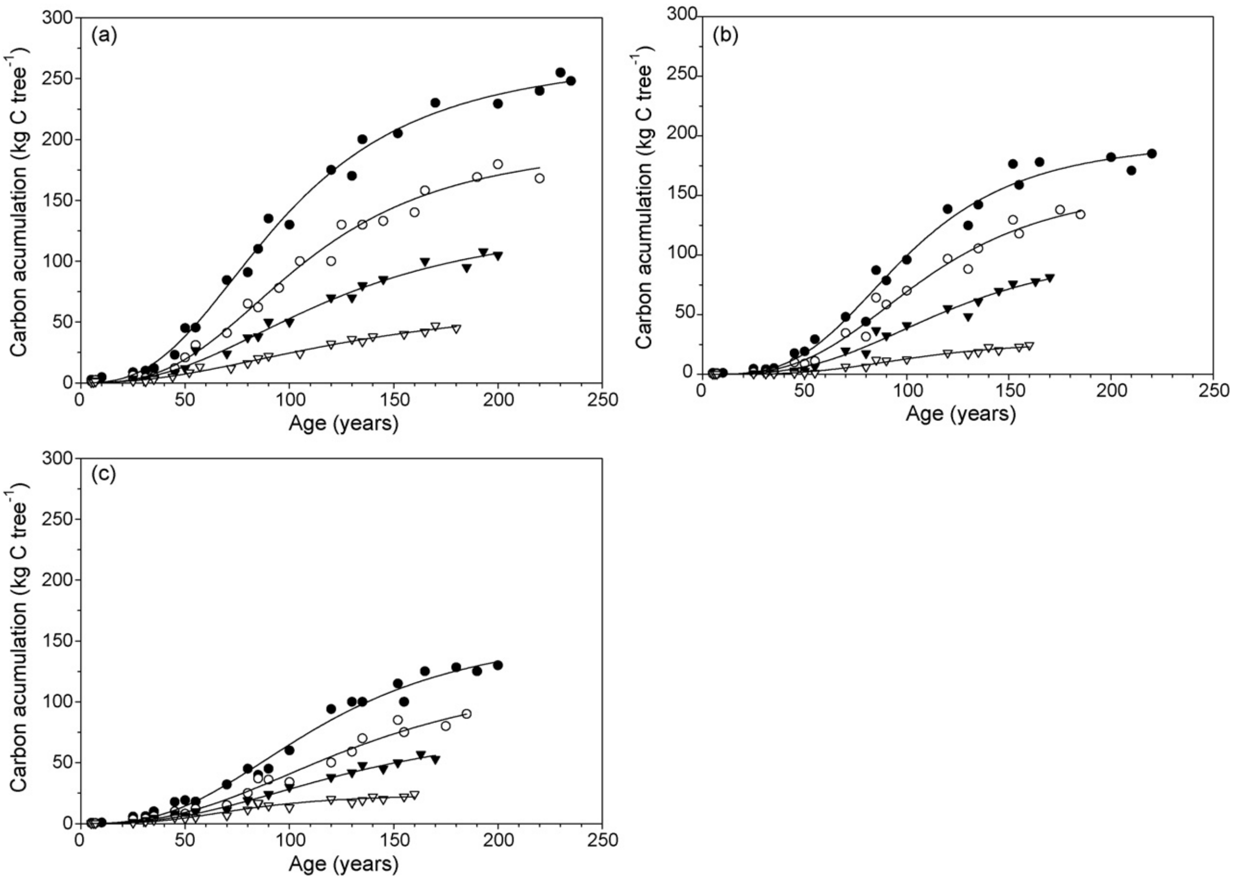

Fig. 1. Total carbon accumulation (kg C tree^{-1}) against age for different crown classes of *Nothofagus antarctica* growing at Site Class III (a), Site Class IV (b) and Site Class V (c), Patagonia. (●) dominant trees, (○) codominant trees, (▼) intermediate trees, (▽) suppressed trees. Site Class III: stands where the mean total height of dominant mature tree (H) reach 10.2 m, Site Class IV: H = 7.8 m, Site Class V: H = 5.3 m.

respectively (Fig. 3). Thus, root C accumulation was greater during the regeneration phase, and then the above-ground C accumulation of young and mature trees increased over time. At any time, the root C accumulation was greater for trees growing on the poorer sites (SC V) than for better site conditions (Fig. 3).

3.5. C allocation in tree components

Significant differences were found in C distribution between components (Table 4), e.g. mature trees allocated more C mainly to sapwood and heartwood and less to fine roots. C allocation varied significantly according to tree age, e.g. mean C allocation for dominant trees in the regeneration phase growing on SC IV was mainly to medium roots (41.1%) and 30.1% of C was allocated to sapwood in mature dominant trees for the same site quality (Table 4). C allocation also varied according to the site quality, e.g. there was a decrease in C storage in leaves, small branches, sapwood, bark and fine roots of trees grown on the better sites (SC III) compared to poorer sites (SC V) (Table 4). In general, there was a significant difference in C allocation between crown classes in leaves and small branches components (except sapwood in SC IV) (Table 4).

3.6. Estimation of C storage at stand level

The equations for total C accumulation from individual trees were used to estimate the C storage at the stand level using forest inventory data. Total C storage in *N. antarctica* forest ranged from 40.3 Mg C ha^{-1} for mature stands grown at SC V to 182.0 Mg C ha^{-1} for optimal growth stands at SC III (Table 5). In all studied site quality classes, total C accumulation was greater at the development stage of optimal growth (21–110 years). Sapwood contained more C in SC III (66.4 Mg C ha^{-1}) than SC IV (32.5 Mg C ha^{-1}), while medium roots contained more C in the SC V (15.8 Mg C ha^{-1}) stands.

4. Discussion

4.1. C concentrations

A C concentration of 50% in dry biomass components of trees is widely used as a constant conversion factor for C stock estimation (Bert and Danjon, 2006). In the present study, mean tissue C concentration varied from 46.3% in medium roots of dominant trees to 56.1% in rotten wood for trees grown in SC V. This range is slightly lower than that for ten temperate tree species in China (43.4–55.6%) (Zhang et al., 2009), but it is wider that those described for 41 North America tree species (46.3–55.2%) (Lamlom and Savidge, 2003). Therefore, tree age, crown class and site quality of the stands need to be considered to provide an accurate forest C stock estimation for *N. antarctica*. For example, when using the general default value of 50% C concentration, it was calculated that total C accumulation of individual trees had been on average underestimated by 1.1% and C accumulation in roots overestimated by 1.4% of most of the observed data (Figs. 1 and 3).

C concentration in tree components decreased from dominant to suppressed trees. There are no reports of C concentrations in relation to the degree of crown suppression for *N. antarctica*. These changes are consistent with Lambers et al. (1998) who reported that plants have greater C concentrations of 'least expensive' (in terms of ATP required for biosynthesis) structural carbohydrates and lignin compounds when growth conditions become less favourable com-

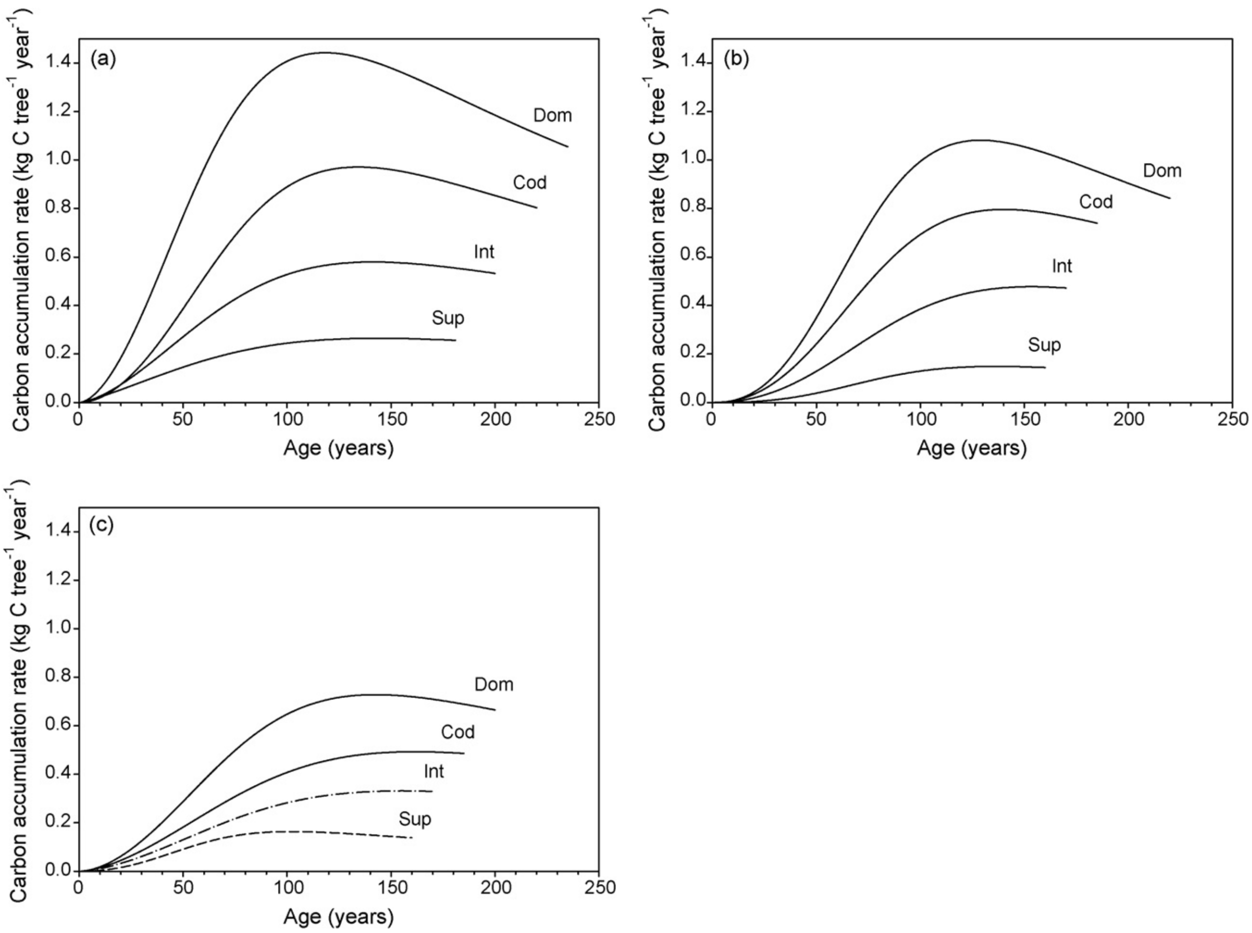

Fig. 2. Carbon accumulation rates (kg C tree^{-1} year^{-1}) for *Nothofagus antarctica* trees against age sorted by four crown classes. (a) Site Class III, (b) Site Class IV, and (c) Site Class V. Site Class III: stands where the mean total height of dominant mature tree (H) reach 10.2 m, Site Class IV: H = 7.8 m, Site Class V: H = 5.3 m.

pared with high concentration of 'most expensive' lipid and protein compounds characteristic of fast-growing species. Furthermore, tissues of fast-growing species that have high protein concentrations (an expensive constituent) also have greater concentration of minerals (Poorter, 1994). In this context, dominant trees have a larger crown and root system that may increase their growth rate

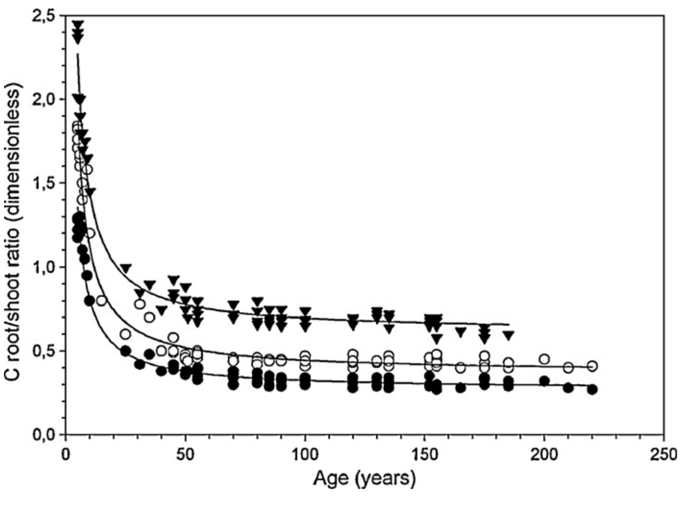

Fig. 3. Carbon root/shoot ratio for *Nothofagus antarctica* trees against age. (●) Site Class III, (○) Site Class IV, and (▾) Site Class V. Site Class III: stands where the mean total height of dominant mature tree (H) reach 10.2 m, Site Class IV: H = 7.8 m, Site Class V: H = 5.3 m.

and consequently may decrease the components C concentration in components of trees. This explanation may be applied to the greater C concentration in the poorer site quality (SC V) compared with trees grown in better environmental conditions (SC III). This is consistent with Zhang et al. (2009) who reported that mean C concentration was negatively correlated to mean annual increment of tree biomass. Jaramillo et al. (2003) reported that while C concentrations did not vary among above-ground components of Mexican tropical dry forests, root C concentrations ranged from 33.4 to 43.4% across all sites and size classes.

C concentration in sapwood, heartwood, bark, fine and coarse roots components of *N. antarctica* trees increased with age from regeneration to mature development stages. There is a continued increase in the proportion of cell wall components, e.g. carbonated structures as trees become older (Lambers et al., 1998). Tissues had different C concentrations in *N. antarctica*. C concentration graded in the following order: heartwood > rotten wood > sapwood > bark > small branches > coarse roots > leaves > medium roots > fine roots. Zhang et al. (2009) also reported that C concentration of fine roots was the lowest (47.1%) among the biomass tissue of 10 temperate tree species.

4.2. Total C accumulation and allocation in tree components

Total C accumulation of individual trees was empirically derived and summarized into easily transferable coefficients using non-linear regression. Total C accumulation for individual trees of *N. antarctica* was affected by tree age, crown class and site quality. Total C accumulated for mature dominant trees was six times

Table 4
Carbon allocation (%) in components of *Nothofagus antarctica* trees for different crown, age and site classes. Data were expressed as percentage of biomass. Site Class III: stands where the mean total height of dominant mature tree (H) reach 10.2 m, Site Class IV: H = 7.8 m, Site Class V: H = 5.3 m.

Age classes	Crown class	Leaves	Small branches	Sapwood	Heartwood	Bark	Rotten wood	Roots		
								<2 mm	<30 mm	>30 mm
Site Class III										
111–235 years	D	4.2	6.4	33.0	19.5	11.0	0.9	0.8	3.7	20.5
	C	3.5	6.6	30.8	19.9	11.5	1.1	0.9	3.5	22.2
	I	2.5	7.5	33.0	18.1	10.8	2.3	0.7	3.2	21.9
	S	1.9	4.8	30.2	17.5	8.1	9.8	0.6	3.8	23.3
21–110 years	D	7.6	12.4	34.0	5.5	9.8	0.0	2.0	8.9	19.8
	C	7.3	11.4	34.4	6.5	9.2	0.0	1.8	9.3	20.1
	I	6.0	12.8	38.1	4.8	8.0	0.0	1.6	9.2	19.5
	S	5.2	11.4	39.4	4.4	8.8	0.0	1.3	10.5	19.0
5–20 years	D	7.2	18.4	16.0	0.0	4.4	0.0	2.2	33.5	18.2
	C	6.8	18.5	14.5	0.0	4.0	0.0	2.3	35.9	18.0
	I	5.2	19.7	17.1	0.0	3.0	0.0	2.3	34.9	17.8
	S	4.7	17.4	16.2	0.0	5.4	0.0	2.2	36.2	17.9
Age class effect		*	**	*	**	**	**	*	**	*
Crown class effect		**	*	ns	ns	ns	ns	ns	ns	ns
Site Class IV										
111–220 years	D	2.2	4.8	30.1	21.7	9.1	1.3	0.5	4.8	25.6
	C	0.9	1.9	19.1	31.7	14.9	1.5	0.6	4.7	24.9
	I	1.3	2.7	18.5	30.4	14.6	2.3	0.5	4.7	25.0
	S	1.6	4.7	27.5	20.4	12.9	2.3	0.7	4.4	25.4
21–110 years	D	6.2	11.9	34.9	2.1	10.7	0.0	1.1	10.5	22.6
	C	4.7	8.5	34.5	9.9	9.2	0.0	1.1	10.1	22.0
	I	2.8	7.1	39.4	7.4	10.2	0.1	1.0	10.1	21.9
	S	2.5	5.8	39.1	7.5	12.3	0.1	0.9	10.0	21.8
5–20 years	D	6.5	13.6	12.6	0.0	4.0	0.0	5.2	41.1	17.0
	C	5.3	12.9	11.9	0.0	4.2	0.0	5.3	43.4	17.0
	I	4.1	15.8	12.4	0.0	4.1	0.0	5.1	41.9	16.6
	S	4.0	16.4	11.3	0.0	5.0	0.0	5.2	41.5	16.7
Age class effect		**	**	*	**	*	**	**	**	*
Crown class effect		*	*	*	ns	ns	ns	ns	ns	ns
Site Class V										
111–200 years	D	1.2	3.2	20.2	25.0	8.4	2.1	0.3	5.9	33.7
	C	1.7	4.5	17.1	24.7	9.1	2.5	0.2	5.4	34.8
	I	2.4	4.8	15.5	27.4	9.3	3.1	0.1	5.2	32.2
	S	1.1	4.2	14.1	28.0	9.4	5.5	0.2	6.0	31.4
21–110 years	D	3.9	8.2	25.9	5.0	7.6	0.3	3.1	15.4	30.5
	C	3.4	9.1	24.2	6.5	8.0	0.5	2.8	15.7	29.8
	I	3.9	8.5	23.8	7.0	9.6	1.3	2.7	14.8	28.4
	S	2.8	16.2	22.9	4.0	8.7	1.6	2.6	13.3	28.0
5–20 years	D	3.7	13.2	11.5	0.0	4.8	0.0	8.6	38.2	20.0
	C	3.0	12.3	10.3	0.0	4.1	0.0	9.3	41.2	19.8
	I	2.8	12.5	9.9	0.0	4.2	0.0	9.4	40.1	21.1
	S	1.9	13.2	8.5	0.0	5.3	0.1	6.2	44.0	20.8
Age class effect		**	**	*	**	*	**	**	**	*
Crown class effect		*	*	ns	ns	ns	*	ns	ns	ns

D: dominant trees, *C*: codominant trees, *I*: intermediate trees, *S*: suppressed trees.
ns = non significative.
* $P < 0.05$.
** $P < 0.01$.

greater than mature suppressed trees, and total C accumulated by mature dominant trees grown at SC III was doubled that for SC V stands. The greater C accumulation of dominant trees at any age compared to inferior crown classes was very closely related to the C accumulation rates. This is consistent with Rötzer et al. (2009) who estimated that the amount of C storage in both above- and below-ground components over time for a mixed beech stand changed with variations in site conditions, especially when temperature and radiation increased and precipitation decreased. Dominant trees and trees growing in better site qualities had larger crowns with more biomass of photosynthetic green leaves, and consequently had faster growth rates. In contrast, the leaves of suppressed trees located in the inferior stratum receive less available light for photosynthesis and these less active leaves may accumulate less C. Also, crown classes and site quality of *N. antarctica* stands affected the moment of maximum C accumulation, which was later for suppressed trees compared with dominant trees, and earlier for trees growing on better quality sites than poor quality sites.

C allocation varied significantly according to tree age and site quality. This was mainly due to inferior crown classes or trees grown in poor quality sites developing more structural tissues with lignin in bark, branches and stem components, combined with low foliage biomass. Similarly, Swamy et al. (2003) reported that C storage in different components of a *Gmelina arborea* plantation

Table 5
Predicted amount of carbon (Mg C ha^{-1}) in sampled *Nothofagus antarctica* stands in Southern Patagonia.

Stand	Leaves	Small branches	Sapwood	Heartwood	Bark	Rotten wood	Roots <2 mm	Roots <30 mm	Roots >30 mm	Total
Site Class III										
Regeneration	4.6	9.6	48.3	28.5	15.7	5.4	1.1	5.4	33.4	152.1
Optimal growth	11.9	21.8	66.4	9.6	16.3	0.0	3.0	17.2	35.7	182.0
Mature	4.5	13.9	12.0	0.0	3.2	0.0	1.7	26.4	13.5	75.1
Site Class IV										
Regeneration	0.8	2.0	13.4	14.6	7.2	1.0	0.3	2.6	14.2	56.2
Optimal growth	3.6	7.3	32.5	5.9	9.3	0.0	0.9	8.9	19.4	87.9
Mature	2.9	8.6	7.1	0.0	2.5	0.0	3.0	24.6	9.9	58.6
Site Class V										
Regeneration	0.8	2.1	8.4	13.2	4.6	1.7	0.1	2.8	16.6	50.3
Optimal growth	1.9	5.7	13.1	3.0	4.6	0.5	1.5	8.0	15.8	54.0
Mature	1.1	5.2	4.1	0.0	1.9	0.0	3.4	16.5	8.2	40.3

Site Class III: stands where the mean total height of dominant mature tree (H) reach 10.2 m, Site Class IV: H = 7.8 m, Site Class V: H = 5.3 m.

showed significant variation due to differences in age and site. Roots were the component that accumulated more C, mainly in dominant trees at the regeneration stage and in poor quality sites where root system play an important role in the establishment and nutrient uptake (Lambers et al., 1998). C distribution in *N. antarctica* components contrast with Benecke and Evans (1987) who reported that *N. solandri* var. *cliffortioides* and *N. truncata* trees allocated more fixed carbon to aerial components, especially in photosynthetic organs (28–29% in foliage, 19–29% in shoots and branches, 24–26% in main stem, 5–8% in coarse roots, 12–20% in fine roots), and with Vucetich et al. (2000) who found that the proportion of C allocated to the below-ground components of *Pinus sylvestris* forests did not show any trend across a latitudinal gradient.

4.3. C root/shoot ratio

There are few studies that have reported C both in above- and in below-ground components from which root/shot C ratios can be derived. In *N. antarctica*, this ratio decreased from its maximum value for the regeneration phase to a steady-state asymptote beyond 60 years of age. Thus, C accumulation in roots was greater during the regeneration phase, and then above-ground accumulation of C by mature trees increased over time. Our findings are in agreement with previous studies conducted by Peichl and Arain (2007) who reported that root biomass (and therefore C) decreased with age until the stand reached a constant root/shoot ratio. This contrasts with Vanninen et al. (1996) who reported that the below-ground component was fairly independent of tree age. The above-ground C content for *N. antarctica* was lower than values reported by Hart et al. (2003) for an even-aged *N. truncata* old-growth forest (~75% of the total C with a root/shoot ratio of 0.28).

We also found differences in the C root/shoot ratio of individual trees between site classes with C accumulation in roots being greater at any time for trees growing on poorer sites (SC V) than for better site conditions. It is possible that *N. antarctica* has more root biomass to ensure establishment during stand replacement to improve water and nutrient uptake in dry environments and to provide better support in windy sites with shallow soils, compared to other *Nothofagus* species.

4.4. Soil and stand C accumulation

Total C content in the soil profile varied according to the site quality, and did not varied significantly with stand age. This is consistent with Davis et al. (2003) who reported that the sum of forest floor and mineral soil C in a New Zealand *Nothofagus* forest did not differ with age. The differences between site quality of the stands found in the present work were mainly due to a greater litter C content at the best sites mainly because litterfall was greatest and for the increasing gradient in soil C concentration from SC V to SC III that influenced C content in organic and inorganic horizons. The differences found in C concentration in litter and organic layers between sites could be a result of differences in the chemical composition of the tree litter or differences in proportions of litter additions from foliage and branches (Alriksson and Erikson, 1998). The C in the soil pool (Table 2) represents between 52% (optimal growth phase stand grown at SC IV) and 73% (mature phase stand grown at SC III) of total ecosystem C. This is in contrast with Finér et al. (2003) who reported that most of the C pool (62%) of old-growth Norway spruce-dominated stands was mainly in living trees. The soil C pool estimated in the present work was greater than those reported for other *Nothofagus* species (Tate et al., 1993; Hart et al., 2003) and similar to native cypress forests in Patagonia (Laclau, 2003). Therefore, there is a need to understand the variability in soil C storage among forest types.

Total C accumulation at stand level was determined by growth phase, stocking, crown class proportions and site class, e.g. the amount of C was greater in a young primary forest stand compared with an older one characterized by a lower stocking and biomass. Similarly, Davis et al. (2003) estimated that stem C storage in *N. solandri* var. *cliffortiodes* forest in a montane zone of New Zealand reached a maximum value (137 Mg C ha^{-1}) at the pole development stage (120 years), and also in agreement with Jaramillo et al. (2003) who reported that total C pools in Mexican forests varied according to site quality from 141 Mg C ha^{-1} in dry forest to 306 Mg C ha^{-1} in floodplain stands. Also, Vucetich et al. (2000) reported that total C of *P. sylvestris* stands of similar age, elevation and species composition increased from 79 to 187 Mg C ha^{-1} in a latitudinal gradient associated with increasing annual temperature and rainfall. In contrast, Silvester and Orchard (1999) reported that C storage of Kauri (*Agathis australis*) forest (aboveground and forest floor) increased with age from 64 Mg C ha^{-1} for a regenerating pole stand to 990 Mg C ha^{-1} for mature forest. Laclau (2003) also reported that C storage of native cypress forest in northwest Patagonia did not change significantly with stand age and precipitation (site quality). In particular, roots accounted for 26% (regeneration phase grown at SC III) to 72% (mature phase grown at SC V) of total C in living trees of the stands (Table 5). In contrast, Hart et al. (2003) working with mature *N. truncata* forest growing on a better site quality (dominant height of 21 m) estimated greater amounts of C in the above- than the below-ground components (165.9 vs. 46.7 Mg C ha^{-1}).

The use of functions provides a valuable tool for understanding and estimating C accumulation, as well as C root/shoot ratios of primary forests of *N. antarctica* using forest inventories data. Estimates of native forest C storage are required for estimating regional and national greenhouse gas balance. Information of above- and below-ground C accumulation related to age and crown classes for *N. antarctica* have not been previously reported and therefore the present work provided new knowledge. Thinning in silvopastoral systems may change the distribution of C allocation within a stand, due to reduction in the number of trees and return of C from litter. Stem-only harvesting rather than whole-tree removal, together with debarking the stem *in situ*, may reduce the loss of soil C pool from the forest ecosystem. Furthermore, root systems from removed trees remain in the system, and could provide C to soil through decomposition. Therefore, for any particular forest management system it is important to analyse the development of both above- and below-ground C over the forest life cycle for different site qualities for accurate quantification of C pools on regional scale.

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Appendix A.

Parameters of the logistic function (Eq. (1)) for total carbon accumulation of *Nothofagus antarctica* trees. *D*: dominant, *C*: codominant, *I*: intermediate, *S*: suppressed trees. Site Class III: stands where the mean total height of dominant mature tree (H) reach 10.2 m, Site Class IV: H = 7.8 m, Site Class V: H = 5.3 m.

	a	*b*	*c*	R^2	ESE
					SiteClassIII
D	270.2726	−2.7111	97.0055	0.9685	5.6545
C	198.7561	−2.9083	107.5396	0.9778	4.4517
I	135.5965	−2.5210	119.5705	0.9857	3.7963
S	69.3452	−2.2132	131.5974	0.9458	1.6728
					SiteClassIV
D	197.9876	−3.3789	99.7508	0.9842	8.9682
C	162.2860	−3.2102	109.6277	0.9835	6.5961
I	107.4877	−3.1330	120.4181	0.9789	4.4120
S	28.2356	−3.5395	104.7410	0.9781	1.3534
					SiteClassV
D	162.4129	−2.7702	115.9879	0.9941	5.7175
C	129.2757	−2.6032	134.7408	0.9806	4.3958
I	83.7143	−2.5960	129.7488	0.9639	2.3147
S	24.5845	−3.1286	80.3045	0.9860	1.6432

Appendix B.

Parameters of the inverse function (Eq. (2)) for the carbon root/shoot ratio of *Nothofagus antarctica* trees. Site Class III: stands where the mean total height of dominant mature tree (H) reach 10.2 m, Site Class IV: H = 7.8 m, Site Class V: H = 5.3 m.

	a	*b*	R^2	ESE
Site Class III	0.2712	5.4121	0.9826	0.0475
Site Class IV	0.3709	7.4936	0.9759	0.0658
Site Class V	0.6135	8.2782	0.9955	0.0694

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